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Description of advertisement calls of six species of the genus *Chaparana* (Ranidae) from Nepal and India

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The advertisement calls of six species of the genus *Chaparana* (subgenus *Paa*) are described in details, those of two of them (*Chaparana minica* and *Chaparana vicina*) for the first time. For each species various temporal and frequency parameters are given. Each call is illustrated by an oscillogram, a spectrogram and a spectrum. The general characteristics of these peculiar calls are discussed as adaptations to a noisy torrent environment. The calls and modes of life of these frogs are consistent with their taxonomy based on morphological and molecular characters.

INTRODUCTION

This paper is devoted to the description of the advertisement calls of six species of the subgenus *Paa* of the genus *Chaparana* Bourret, 1939, as redefined by OHLER & DUBOIS (2006). This genus of the ranid tribe Paini (DUBOIS, 1992, OHLER & DUBOIS, 2006) includes 26 species distributed in South and Southeast Asia (Pakistan, India, Nepal, western China through Myanmar, Thailand, Laos, Cambodia and Vietnam) (DUBOIS, 1976, FROST, 1985; FEI, 1999). The species of the genus *Chaparana* are torrent-living species. The males of these species usually call at night from the bed of the torrent, very often hidden under stones and rocks or below the bank, more rarely sitting in the water in more open places of the torrent bed (DUBOIS, 1976, 1977*b*). They are distributed along the torrent which avoids interactions between them (DUBOIS, 1977*b*). The loud and continual background noise of the running water as well as their calling sites triggered the frogs to develop an advertisement call adapted to this environment, a type of call seldom encountered in the other species of Ranidae, except for those living in the same kind of habitats, such as *Amolops* (DUBOIS, 1977*a*). The calls of some of the species described hereafter have already been briefly described by DUBOIS (1977*b*). We decided to redescribe them to provide parameters which were not measured at that time and to give standard descriptions of calls which can be used for comparison in future studies.

The calls of six species of *Chaparana (Paa)* were recorded during field work in Nepal and India by the second author in 1972, 1973 and 1977 (tab. 1). However, the distributions of these species are larger: *Chaparana (Paa) rostandi* lives in Nepal only, *Chaparana (Paa) vicina* occurs in India and Pakistan, *Chaparana (Paa) mimica* in India and Nepal, and *Chaparana (Paa) blanfordii*, *Chaparana (Paa) liebigii* and *Chaparana (Paa) polunini* are found in Nepal and China (Dubois, 1976, 1980, 2000, Frost, 1985). They are all mountain species which occur mostly at high altitudes.

Material and methods

Recordings (tab. 1) were made using either a Uher Report 4000 or a Sony TCDM-5 tape recorders, and Scotch magnetic 215 and TDK SA-X90 tapes. Oscillograms, spectrograms and spectrums were prepared with the software tool Canary 1.2 from the Cornell Laboratory of Ornithology (Charif et al., 1995). The sampling rate used to convert the signals to digital format was 22 254 Hz with 16-bit precision. A filter bandwidths of 349.70 Hz and frame length of 512 points were used for both spectrogram and spectrum analyses.

The following measurements were taken from the oscillogram: duration of calls (dc), duration of notes (dn) and intervals between notes (din), number of notes per call (nn) and note rate (number of notes per second, nns). Frequency measurements were made from the spectrum of a few notes within the signals. The frequency values given (in text and tab. 2) are the means of the values of the same frequency band of those notes. The visible frequency bands are noted f1b to f5b (when possible) from the fundamental frequency to the highest harmonic.

The recording of the call of *C. vicina* was interfered by a significant background noise. So we used the software Signalyse 3.10 which proves to be more efficient to filter signals: frequencies below 300 Hz and above 500 Hz were cut off, oscillograms and spectrogram were built with Canary 1.2. The call of *C. mimica* was recorded with deficient batteries in the tape recorder. So one can hear an important speed difference when the tape is played with a Uher in good condition. The tape was re-recorded using the human voice on the tape as an indication for the adequate speed (original speed 17.6 cm/s instead of 19.0 cm/s, that is to say 7.5 % of the normal speed). Therefore there is a probable (slight) error on the measurements of the parameters for time and frequency. The latter should be considered with caution and rounded off (the margin of error could not be estimated). However it seemed useful to publish a description of this call as data concerning this species are rare.

All the specimens are deposited in the collection of the Muséum National d'Histoire Naturelle of Paris (MNHN).

Except for *C. vicina*, no males whose calls are studied here could be caught, so it is impossible to give a voucher number for each animal. Snout-vent lengths were estimated by averaging the snout-vent lengths of males caught in the same population as the singer (Dubois, pers. obs.). The MNHN collection numbers of the individuals taken into consideration for calculation of the means are the following: (1) *C. blanfordii*, 1975.1056-1058, (2) *C. liebigii*, 1975.1093, 1975.1097-1098, 1975.1102, 1975.1105-1107, 1975.1109-1112, (3)

Table 1. List of the species studied with information on the place and date of recording. Air T°: air temperature, Water T°: water temperature.

Species	Date and hour of recording	Country	Locality	Coordinates	Altitude	Air T°	Water T°
Chaparana (Paa) blanfordii (Boulenger, 1882)	05.05.1973, 19h25-22h00	Nepal	Lam Pokhari	27°06'N, 87°59'E	2910 m	No data	No data
Chaparana (Paa) liebigii (Gunther, 1860)	25.06.1973, 20h30	Nepal	Ghat	27°43'N, 86°43'E	2510 m	15.0°C	14.5°C
Chaparana (Paa) minica (Dubois, 1975)	03.08.1977, 22h50	India (Himachal Pradesh)	Katrain	32°08'N, 77°09'E	1530 m	21.0°C	24.0°C
Chaparana (Paa) polunini (Smith, 1951)	23.06.1973, 20h20	Nepal	Thammu	27°49'N, 86°41'E	3360 m	12.5°C	11.5°C
Chaparana (Paa) rostandi (Dubois, 1974)	21.08.1972, 23h00	Nepal	Kalopani	28°38'N, 83°36'E	2540 m	16.0°C	No data
	04.09.1972	"	"	"	"	14.5°C	11.5°C
	31.08.1972, 20h40-21h00	"	Kutsab Terna Tal	28°46'N, 83°43'E	2890 m	16.5°C	19.0°C
Chaparana (Paa) vicina (Stoliczka, 1872)	10.07.1977	India (Jammu & Kashmir)	Patnitop	33°02'N, 75°20'E	2050-2060 m	19°C	No data

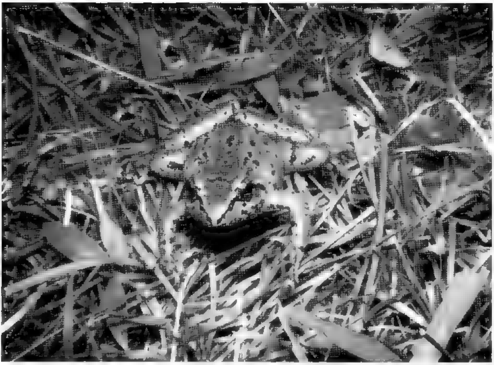

Fig. 1. — *Chaparana (Paa) blanfordii* (Boulenger, 1882), female MNHN 1975.1056, Chauki (East Nepal), 15 July 1973.

C. minica: 1989.2057-2058, 1989.2060, 1989.2062, 1989.2064-2067, 1989.2069-2070, 1989.2072, 1989.2075, 1989.2077-2083; (4) *C. polunini*: 1975.1441-1446, 1975.1457-1458; (5) *C. rostandi* (Kalopani), 1975.959, 1975.962-964; *C. rostandi* (Kutsab Terna Tal): 1973.310, 1973.320-321; (6) *C. vicina*: 1985.1047.

Dates and times of recordings are provided in tab. 1, together with the data on temperature (air and water) when available.

RESULTS

CHAPARANA (PAA) BLANFORDII (Boulenger, 1882)

Chaparana blanfordii (fig. 1) was recorded during the rainy season in a humid forest rich in small torrents, where calls could be heard all around both during day and night. The call was recorded at night in a small torrent running under trees. The males were calling from the bed of the forest torrent hidden between rocks, so not directly from the ground. Several males were calling widely spaced in this torrent.

The call of this species (fig. 2, tab. 2) is short, high-pitched and repetitive. It consists in continuous series of 15-17 short amplitude modulated notes with two lobes (0.026 s

Table 2 Characteristics of the advertisement call of *Chaparana (Paa) blanfordii* and *Chaparana (Paa) liebigii* from Nepal, *Chaparana (Paa) minica* from India, *Chaparana (Paa) polunini*, *Chaparana (Paa) rostandi* and *Chaparana (Paa) vicina* from Nepal. Only one male was recorded for each species except for *P. rostandi* whose calls of three different males were recorded

SVL, male snout-vent length, dc, duration of sequences from first to last note, dic, duration of silent intervals between two consecutive sequences, dn, duration of notes, din, duration of silent intervals between two consecutive notes; nn, number of notes per call; nns, number of notes per second; f*i*b, frequence of the band *i*. Snout-vent lengths are expressed in mm, time measurements in seconds and frequencies in Hz. Value are given as: mean ± standard deviation, minimum-maximum, number of measurements.

Species	SVL	dc	dic	dn	din	nn	nns	f1b	f2b	f3b	f4b	f5b
Chaparana blanfordii (Lam Pokhari)	40.4 ± 2.0 38.5-42.5 3	3.96 ± 0.44 3.65-4.27 2	–	0.025 ± 0.009 0.010-0.044 32	0.236 ± 0.019 0.208-0.276 30	16.0 ± 1.4 15-17 2	4.1 ± 0.1 4.0-4.1 2	1529 ± 37 1469-1548 8	3076 ± 102 2860-3194 7	4631 ± 87 4487-4741 8	–	–
Chaparana liebigii (Ghat)	70.1 ± 9.7 56.4-89.5 11	2.26 ± 0.02 2.25-2.28 2	–	0.021 ± 0.003 0.016-0.026 31	0.130 ± 0.032 0.097-0.254 29	15.5 ± 0.7 15-16 2	6.9 ± 0.2 6.7-7.0 2	730 ± 52 686-784 9	–	–	–	–
Chaparana minica (Katrain)	34.5 ± 1.8 31.2-37.2 9	3.83 ± 0.91 3.0-5.5 6	–	0.087 ± 0.017 0.044-0.127 81	0.207 ± 0.061 0.124-0.466 72	13.5 ± 3.0 10-19 6	3.5 ± 0.2 3.3-3.8 6	1134 ± 43 1097-1215 20	2274 ± 78 2136-2410 20	3430 ± 116 3252-3625 17	4497 ± 116 4310-4643 10	5639 ± 116 5486-5780 9
Chaparana polunini (Thammu)	39.7 ± 2.3 37.3-43.6 8	1.06 ± 0.06 0.99-1.11 3		0.019 ± 0.007 0.003-0.030 31	0.093 ± 0.25 0.073-0.210 28	10.3 ± 0.6 10-11 3	9.8 ± 0.4 9.3-10.1 3	1642 ± 0 8	3274 ± 11 3260-3284 4	4954 ± 45 4902-4995 6	–	
Chaparana rostandi (Kalopani)	51.7 ± 5.3 46.0-58.7 4	0.73 ± 0.10 0.66-0.80 2	–	0.055 ± 0.006 0.046-0.061 7	0.216 ± 0.029 0.186-0.255 5	3.5 ± 0.7 3-4 2	4.8 ± 0.3 4.5-5.0 2	1593 ± 104 1371-1646 7	3138 ± 247 2645-3272 7	4686 ± 326 4056-4918 6	–	–
Chaparana rostandi (Kalopani)	51.7 ± 5.3 46.0-58.7 4	0.93 ± 0.15 0.83-1.04 2		0.054 ± 0.012 0.029-0.068 11	0.144 ± 0.016 0.127-0.177 9	5.5 ± 0.7 5-6 2	5.9 ± 0.2 5.8-6.1 2	1949 ± 165 1646-2077 11	3923 ± 378 3194-4212 9	6178 ± 117 6034-6289 6		
Chaparana rostandi (Kutsab Terna Tal)	49.8 ± 1.0 49.0-50.9 3	0.6	–	0.059 ± 0.005 0.055-0.065 4	0.131 ± 0.012 0.124-0.145 3	4	6.3	1641 ± 120 1469-1724 4	3262 ± 232 2919-3429 4	4883 ± 332 4389-5074 4	–	–
Chaparana vicina (Patnitop) MNHN 1985.1047	74.2	0.65 ± 0.12 0.47-0.88 10	5.06 ± 1.62 3.50-7.74 6	0.056 ± 0.021 0.015-0.108 69	0.054 ± 0.023 0.001-0.091 45	6.3 ± 1.0 5-8 11	10	350	700	–	–	–

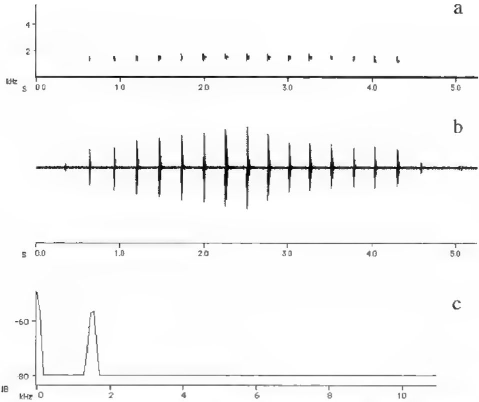

Fig. 2. A sequence of the advertisement call of *Chaparana (Paa) blanfordii* (Boulenger, 1882), Lam Pokhari (East Nepal), 5 May 1973: (a) spectrogram, (b) oscillogram, (c) spectrum of a note in the middle of the call.

in average) whose intensity increases until half or towards the end of the call, and then decreases in the same way. The average call duration is 4.0 s. The note repetition rate is quite slow (four notes per second). The intensity of each note decreases from its start to its end. Each note consists of two lobes, the first one with a large amplitude, the second one with a small one. The dominant frequency corresponds to the first frequency band and it is about 1529 Hz.

CHAPARANA (PAA) LIEBIGII (Günther, 1860)

The recordings of *Chaparana liebigii* were made at night in the Dudh Kosi river bed. The male (fig. 3) could not be caught: it was calling hidden down between blocks close to water in this rather large torrent. The females were often seen close to the males, hidden in cavities between rocks.

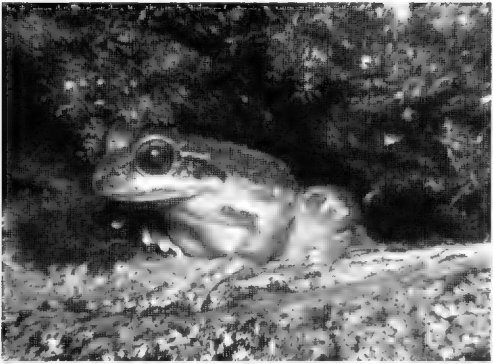

Fig. 3. *Chaparana (Paa) liebigii* (Günther, 1860) male at night in its calling site under rock in the torrent's bed, Ghat (Center-East Nepal), 25 June 1973

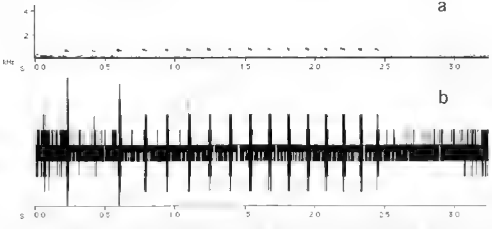

Fig. 4. A sequence of the advertisement call of *Chaparana (Paa) liebigii* (Günther, 1860), Ghat (Center-East Nepal), 25 June 1973, air temperature 15.0°C, water temperature 14.5°C. (a) spectrogram; (b) oscillogram. Note the important background noise due to the torrent

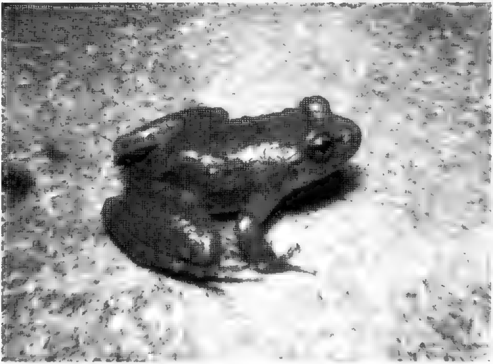

Fig. 5. – *Chaparana (Paa) minica* (Dubois, 1975), male MNHN 1989.2065, Katrain (Himachal Pradesh, India), 4 August 1977.

The call of this species (fig. 4, tab. 2) is a more or less regular succession of 15-16 short notes. It has the same structure as the call of *C. blanfordii* and lasts about 2.26 seconds. The note repetition rate is about 6.8 notes per second and the duration between two successive notes averages 0.134 s. The first note of the call is emitted with higher intensity than the following ones, and the duration of the interval between this note and the next one is longer than the interval between the other notes of the sequence. Because of the loud background noise, only the dominant frequency was measured (about 730 Hz).

CHAPARANA (PAA) MINICA (Dubois, 1975)

Chaparana minica (fig. 5) was recorded at night near a small stream where the males were calling, on the ground, in a basin filled with water. Among the six species studied in this paper, this is the only species in which two or three males were observed singing in a chorus.

Because of the problem encountered during recording (see *Materials and methods*), the values given here in text are rounded off, whereas the values in tab. 2 are reported as measured. The call of this species (fig. 6, tab. 2) consists of long (3.0-5.5 s) sequences, separated by intervals of about ten seconds, and composed of numerous notes (10-19). By its general aspect this call is quite similar to that of *C. liebigii*. Generally, the call of *C. minica* begins by one or

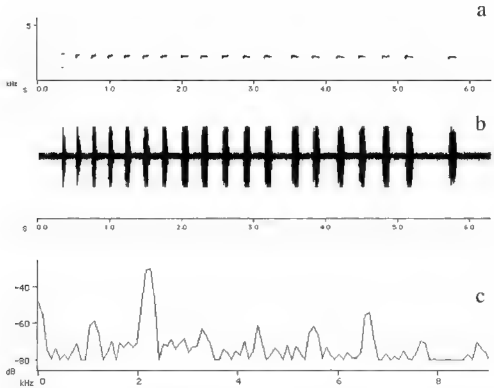

Fig. 6. – A sequence of the advertisement call of *Chaparana (Paa) minica* (Dubois, 1975), Katrain (Himachal Pradesh, India), 3 August 1977, air temperature 21.0°C, water temperature 24.0°C. (a) spectrogram; (b) oscillogram; (c) spectrum of a note in the middle of the call.

two notes shorter and greater in amplitude than the following ones. During the sequence the duration of notes increases (without variation in amplitude), as well as the duration of intervals between notes (this is not an artifact due to problems in the tape speed, as the same values are found in all recorded sequences). The signal stops usually with one or two notes emitted after an interval lasting in average 0.5 s (range 0.4-0.6), i.e., longer than the previous ones. The value of this unusual interval was excluded from the calculation of the mean interval between notes (din) (tab. 2). The amplitude of the notes reaches its maximum at its beginning then decreases gradually. Each note is composed of two parts, the first one, rounded, covering about the first quarter of the total length of the note, the second one, elongate, reaching its maximum amplitude shortly after its beginning, then decreasing slowly. An amplitude modulation, and a rising frequency modulation of about 300 Hz, are present at the beginning of each note. Up to nine frequency bands are visible in the spectrogram. Two frequency bands are more intense than the others: the second frequency band at about 2300 Hz corresponding to the dominant frequency, and the sixth band lying at about 6800 Hz.

Fig. 7. *Chaparana (Paa) polunini* (Smith, 1951), male MNHN 1975.1454, Tesinga (Center East Nepal), 21 June 1973.

Chaparana (Paa) polunini (Smith, 1951)

Calls of *Chaparana polunini* (fig. 7) were heard in the afternoon, at 16h30, under a mossy block with water dripping, along a small steep torrent. The calls started again at 19h00 and were recorded at 20h20.

The call of this species (fig. 8, tab. 2) is structurally similar to that of *C. blanfordii*, i.e., with an increase of intensity of notes until middle of sequence, followed by a decrease in the same way. It is composed of 10-11 short notes (about 0.020 s) separated by intervals of about 0.1 s. Each note consists of two parts, the former with a great amplitude and a rapid rise and fall, and the latter with a small amplitude. The dominant frequency corresponds to the first frequency band and is about 1642 Hz. The second harmonic band is ill-defined. The dominant frequency of the third call (emitted by the same individual) is about 200 Hz lower and no harmonic bands are visible.

Chaparana (Paa) rostandi (Dubois, 1974)

Chaparana rostandi was first recorded on 21 August 1972 near Kalopani in the large bed of the Kali Gandaki river. The males (fig. 9) were calling in smaller streams running under the

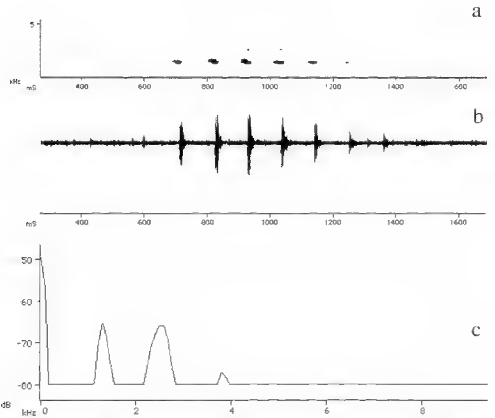

Fig. 8. A sequence of the advertisement call of *Chaparana (Paa) polunini* (Smith, 1951). Thammu (Center-East Nepal), 23 June 1973, air temperature 12.5°C, water temperature 11.5°C. (a) spectrogram; (b) oscillogram, (c) spectrum of a note in the middle of the call.

grassy bank of the river or in puddles under the banks left after decrease of the river level. The male recorded was hidden by grass and bush covering the banks. On 4 September 1972, in the same locality, a single male was calling and was recorded during night.

C. rostandi was recorded again on 31 August 1972 near the lake Katsab Terna Tal (type-locality of the species) at night. The males were calling in the water, under leaves and moss of the bank of the lake covered by vegetation, just below a small forest. Some males called on this bank but none was calling on or under the opposite bank lacking vegetation. The males were spaced out from each other. Other males called sporadically in the puddles, little streams and on the shore of the lake but their calls were not synchronized.

The call of this species (fig. 10, tab. 2) is very short (shorter than or equal to 1 second) and composed of only a few whistled notes (from 3 to 6). The average note repetition rate is 5.7 notes per second. The duration of notes is less than 0.06 s and the intervals between them are of moderate length (from 0.12 to 0.26 s). This call presents a remarkable peculiarity: the last

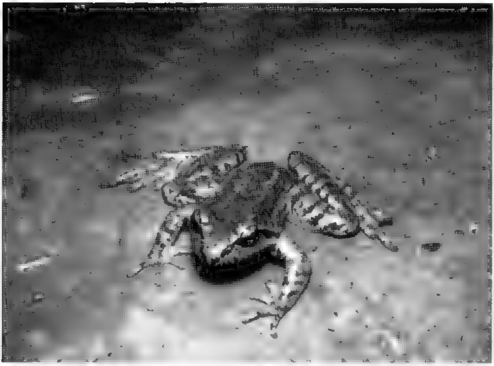

Fig. 9. - *Chaparana (Paa) rostandi* (Dubois, 1974), male MNHN 1975.0964, Kalopani (Northwest Nepal), 22 August 1972.

note of each call has a very notable different tone (there are differences from 100 to more than 400 Hz between the dominant frequency of the last note and that of the others). Furthermore, this note is generally shorter and more damped than the previous ones. Its dominant frequency corresponds to the first frequency band and is about 1745 Hz.

CHAPARANA (PAA) VICINA (Stoliczka, 1872)

The sequences of the advertisement call of *Chaparana vicina* (fig. 11) analyzed were emitted by a single male, hidden under a block in a torrent.

The call of this species (fig. 12, tab. 2) is composed of short sequences (0.65 s) emitted irregularly and separated by intervals of about 5 s. Each sequence consists of a series of 5-8 notes (mean length of note 0.056 s) separated by intervals of 0.05 s on the average. The structure of the notes is similar to that of the notes of *C. blanfordii*. The notes are composed of two bodies linked to each other. Their amplitude increases in the course of the sequence and then decreases very quickly in the last or two last notes. The dominant frequency is about 700 Hz and corresponds to the second band of the spectrogram. The fundamental frequency (or the first band) lies at about 350 Hz.

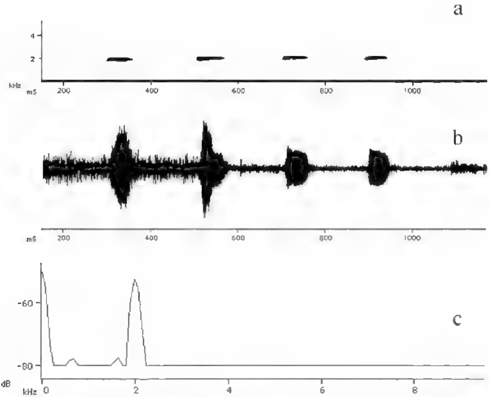

Fig. 10. A sequence of the advertisement call of *Chaparana (Paa) rostandi* (Dubois, 1974), Kalopani (Northwest Nepal), 4 September 1972, air temperature 14.0-14.5°C, water temperature 11.5°C. (a) spectrogram, (b) oscillogram, (c) spectrum of a note in the middle of the call. Note a fluctuation of the background noise during the call.

DISCUSSION

According to their general aspect, the signals of *C. blanfordii* and *C. liebigii* are close to each other, the signal of *C. polunini* appears to be similar to that of *C. vicina*, whereas those of *C. rostandi* and *C. minica* are particular. The calls of the two former species can be distinguished mainly by the values of the frequency bands. The advertisement calls of *C. polunini* and *C. vicina* share only a relatively high note rate (10 notes per second). The call of *C. minica* is particular by the fact that the amplitude of notes does not increase in the first part of sequence and does not decrease in the second half, only the two first notes have a greater amplitude than the others, whereas all the following ones have the same amplitude. The parameters of the calls of several individuals of *C. rostandi* recorded in two different populations show an important variation that covers the values found in other species. For instance the silent interval between the notes of a sequence varies from 130 to 250 ms and overlaps the values of *C. blanfordii* and *C. liebigii*. It is probable that a larger sampling of the

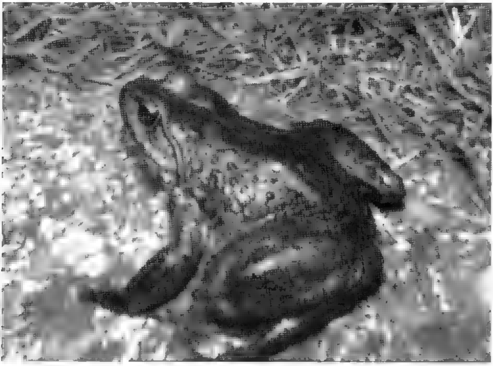

Fig. 11. – *Chaparana (Paa) vicina* (Stoliczka, 1872), male, Manali (Himachal Pradesh, India), 26 July 1977.

other species taken throughout their distribution area would also show a greater variation of each parameter.

Among these species, two are almost sibling species: *C. liebigii* and *C. vicina* (Dubois, 1976, 1980). Except for the male secondary sex characters, their morphologies are very similar, but their advertisement calls are quite different. The call of the former species is longer and composed of more notes than that of the latter species (more than two seconds with about 15 notes in *C. liebigii* in comparison to only half a second with 5-8 notes in *C. vicina*). Differences in notes duration (dn) and interval duration between notes (din) also exist between these two species, but an extended sample of calls could show an interspecific overlap for these parameters. Finally, there is a difference in the frequency, as *C. vicina* has a frequency band below the dominant frequency. Then, even if the two species have an identical dominant frequency, the call of *C. vicina* sounds lower-pitched.

Comparing the bands of dominant frequency of each species, we can notice that *C. liebigii* and *C. vicina* have a very low dominant frequency and *C. minica* a high dominant

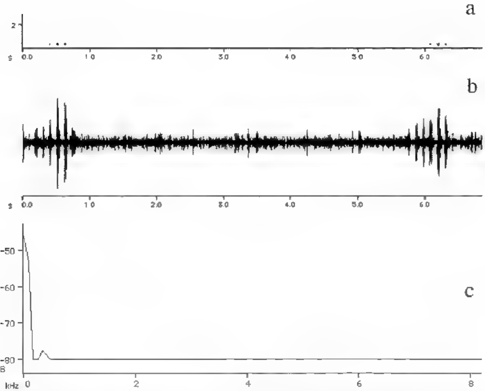

Fig. 12. Two sequences of the advertisement call of *Chaparana (Paa) vicina* (Stoliczka, 1872), Patnitop (Jammu & Kashmir, India), 10 July 1977, air temperature 19°C: (a) spectrogram, (b) oscillogram, (c) spectrum of a note in the middle of the first sequence.

frequency, whereas the three other species cover the same frequency band, i.e., about 1300 Hz to 1850 Hz. This frequency band is surely the best suited to the ecological conditions of these species (see below). Among these three latter species, only *C. polunini* and *C. rostandi* are sympatric in a small area. Therefore other factors must allow the discrimination of the advertisement calls by the females. The frequency of sound is not the only efficient parameter. The duration and shape of the call, the durations between the sequences and other parameters can play a part in the recognition of the specific signal too (PAILLETTE, 1971). The call of *C. rostandi* is markedly different from the other two calls. It has few whistle notes and the last note of each sequence is lower than the previous ones (from 100 Hz to 400 Hz lower pitched than the others). The first note is quite short, the notes in the middle of the call are the loudest and the last one is of lower intensity. The differences between the calls of *C. blanfordii* and *C.*

polunini, which are not sympatric species although both present in Nepal and China (Dubois, 1979; Fei, 1999), are less pronounced.

Little information is available about the advertisement calls of species belonging to the other genera of the tribe Paini as redefined by Ohler & Dubois (2006). The advertisement call of *Quasipaa spinosa* (David, 1875) was briefly described as follows by Pope (1931): "(...) trilled base notes, a sound rivaling in volume and depth that of any frog I have ever heard. Another note is often emitted but it is a weak monosyllable and reminds one of the sound of a hammer brought down upon a small but long pipe filled with water". The call of *Quasipaa exilispinosa* (Liu & Hu, 1975) was briefly described from observations in captivity (Voitel, 2000). It consists in a long series of notes (up to 30), each note lasting about 0.1 s. The value of the dominant frequency has not been specified though the area where frequencies are the most pronounced spreads from 320 to 1920 Hz. The advertisement call of a species of another genus, *Gynandropaa bourreti* (Dubois, 1987), was heard during a field course (Grosjean, pers. obs.). It consists in a series of pulse groups of equal intensity, lasting in total less than ten seconds. The genus *Chaparana* (or at least its subgenus *Paa*) seems to differ from the other genera by an advertisement call rather homogeneous in its gross features.

The species of the ranid tribe Paini are torrent-living species. Their calls are very different from those of other ranid species living in other habitats (Dubois, 1977*a-b*, Dubois & Martens, 1984; Sueur, 1995) and share the same general characteristics. They are characterized by an important particularity: the notes are emitted with a low rate and in more or less long series (from 3 to 19 notes in the calls studied here) separated by relatively long intervals (from 3.5 seconds to one and a half minutes). The notes are very short (from less than 0.010 to 0.127 second) and are separated by short silent intervals (from juxtaposition of notes to 0.466 second). In spite of the weak intensity of calls, these features unquestionably allow a better distinction and localization among the noise of strong streams. This discrimination is likely to work mostly at the beginning and end of sequences.

The main characteristics of these calls have already been discussed (Dubois, 1977*a-b*; Dubois & Martens, 1984). Three major characteristics are common to these calls: (1) the calls are composed of short sequences of notes separated by long periods of silence; (2) the notes are pure, short, and have narrow frequency bands, (3) the notes are rhythmically separated within the sequences.

The calls of torrent-living species belonging to different anuran genera, such as the Oriental *Leptobrachella* (Dring, 1983*a*), *Leptolalax* (Matsui, 1997), *Ansonia* (Dring, 1983*b*; Inger & Dring, 1988) and *Amolops* (Matsui et al., 1993), present the same kind of temporal features. However, differences with the calls of *Chaparana* species also exist, especially in frequency features. Indeed the high dominant frequency of these torrent-living species spreads out on a large frequency band, whereas the calls of *Chaparana* exhibit a low dominant frequency limited to a narrow frequency band. This is found also in some Bolivian torrent-living frog traditionally referred to the genus *Hyla* (Márquez et al., 1993), and placed in the genus *Hypsiboas* by Faivovich et al. (2005). The concentration of energy in a very narrow frequency band, generally the lowest frequency, would provide a greater amplitude to the call and thus favour the propagation of the pure notes over a greater distance, and the signal reception may be more efficient against a background of wide band noise (Chappuis, 1971; Morton, 1975). However, the calls of the *Chaparana* remain of weak intensity and a single

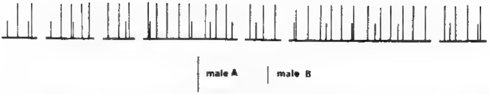

Fig. 13. Diagram showing the succession of the calls of two males of *Chaparana (Paa) polunini* (Smith, 1951) calling close to each other at Thammu (Center-East Nepal), 23 June 1973. Each vertical line indicates the beginning of a sequence of call. The time scale is arbitrary, based on the recorder counter. The breaks on the horizontal line indicate stops in the recording (after DUBOIS, 1977*b*).

rock in the torrent interposed between the observer and the calling frog may be a sufficient obstacle to prevent the frog's call from being heard. The adult males of this genus are distributed along the torrents so that often only the call of a single male can be heard at once by a human observer. The localization of the male is helped in part by the slight binaural discrimination at beginnings and ruptures in the sound emission (MARLER, 1967; FENG et al., 1976, GRIBENSKI, 1977, DUBOIS & MARTENS, 1984, SUEUR, 1995), fast rise and fall times, short durations and moderate repetition rates (LITTLEJOHN, 1977). As a result, the calls of these frogs stand out well on the continuous background noise of the torrent (DUBOIS, 1977*a-b*; DUBOIS & MARTENS, 1984).

The other characteristics found in the *Chaparana* calls, such as a low dominant frequency, a prominent harmonic content and a rapid rise and fall of each note, are shared by some fossorial microhylid frogs' calls from New Guinea (MENZIES & TYLER, 1977) as well as by Australian and Chilean leptodactylid burrowing frogs (LITTLEJOHN & MAIN, 1959, PENGILLEY, 1971, FORMAS, 1985, PENNA & SOLÍS, 1999). These frogs exhibit a dominant frequency lower than 3200 Hz which suits well with the resonance of the burrow and so amplifies the efficiency of the call (BAILEY & ROBERTS, 1981). Other anurans that call hidden from within the ground, such as species belonging to the genera *Alytes* or *Tomodactylus* (DIXON, 1957; MÁRQUEZ & BOSCH, 1995), also share tonal calls with the *Chaparana* species. When the torrents are not in spate, the *Chaparana* call hidden under the rocks. This calling site can be compared to the burrows and subterranean habitats of fossorial frogs. Their notes present a dominant frequency band comprised between 700 and about 2000 Hz (excluding the value of *C. minica*). In all the species studied here, except for *C. minica* and *C. vicina*, the dominant frequency is the fundamental too. The call of *C. minica*, species less rheophilous than the others, which calls from the side of the stream, has a higher dominant frequency.

In most anuran species, during calling period the males synchronize their calls just as if they answered each other. Some species arrange their calls in chorus. This is the case in the European species of the genus *Hyla*, particularly in the well-studied *Hyla meridionalis* (PAILLETTE, 1970, 1976). On the contrary, the males of *Chaparana* studied above, except in *C. minica*, do not answer each other. DUELLMAN (1967) defined different categories of calling behaviour in the light of the social organization of frogs, and named the latter calling behaviour "individual". This behaviour was observed in the field in *C. polunini* (DUBOIS, 1977*b*) and *C. rostandi*, and in playback experiments in *C. blanfordii*. A diagram showing the succession of the call sequences of two males of *C. polunini* that were calling close to each other illustrates this phenomenon (fig. 13). Territorial calls, frequent in paddy-field species and sometimes in forest species (Dubois, 1977*a*), do not seem to exist in the species of this genus. In standard conditions, the males are distributed far from each other, so that only the call of one individual can be heard at once by a human observer. The calls of different males may interfere when the torrents are high, so that the usual shelters of the frogs are flooded. The advertisement calls can have a territorial function so that when a male hears the call of another male he could move away until not hearing it anymore. This function of call has also been assumed in the Papuan microhylids (Menzies & Tyler, 1977).

The call of *C. minica* has the highest dominant frequency of all of the calls analyzed until now, and numerous harmonics. Furthermore, in this species (but also in *C. vicina*), the dominant frequency corresponds to the second frequency band (to the first band in the other four species). These differences with the calls of the other species could be due to the slightly different mode of life of this species. *C. minica* inhabits rather quiet small streams rather than violent torrents and does not call hidden under rocks but on the side of the stream, in puddles. This may explain why the energy of call is not concentrated on a narrow frequency band but spread over a wide range. Furthermore the shape of the advertisement call shows more similarities to the calls of the species inhabiting open areas and some typical features of calls adapted to torrents, such as short duration of notes or variation of amplitude of notes during the call, are not present. Another striking difference to other members of the genus reviewed here is the presence of a chorus like in species living in open areas. So *C. minica* has a habitat and a calling behaviour slightly different from those of the other species considered in this paper. However its call still possesses several features adapted to communication in torrents.

As suggested by Dubois (1977*b*), the strong similarities which exist between the calls of the species studied here more probably express the phylogenetic relationships of these species rather than an evolutive convergence. The constraint imposed by the habitat was presumably the predominant factor responsible for the elaboration of such call features which then were conserved through speciation. A study on American bufonids and hylids (Cocroft & Ryan, 1995) showed that several call parameters can be conserved through repeated speciation events within a homophyletic group.

Résumé

Les chants de six espèces du genre *Chaparana* (sous-genre *Paa*) sont décrits, deux d'entre-eux (*Chaparana minica* et *Chaparana vicina*) pour la première fois. Pour chacune des espèces, de nombreux paramètres de durée et de fréquence sont donnés. Chaque chant est illustré par un oscillogramme, un sonagramme et un spectre. Les caractéristiques générales de ces chants particuliers sont considérées comme des adaptations à un environnement torrenticole. Les chants et modes de vie de ces grenouilles concordent avec les taxons définis par des caractères morphologiques et moléculaires.

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